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SOARING AND GLIDING FLIGHT OF MIGRATING BROAD-WINGED HAWKS: BEHAVIOR IN THE NEARCTIC AND NEOTROPICS COMPARED

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ABSTRACT.—We compared migrating behavior of Broad-winged Hawks (*Buteo platypterus*) at two sites along their migration corridor: Hawk Mountain Sanctuary in eastern Pennsylvania and the Kéköldi Indigenous Reserve in Limón, Costa Rica. We counted the number of times focal birds intermittently flapped their wings and recorded the general flight type (straight-line soaring and gliding on flexed wings versus circle-soaring on fully extended wings). We used a logistic model to evaluate which conditions were good for soaring by calculating the probability of occurrence or absence of wing flaps. Considering that even intermittent flapping is energetically more expensive than pure soaring and gliding flight, we restricted a second analysis to birds that flapped during observations, and used the number of flaps to evaluate factors influencing the cost of migration. Both the occurrence and extent of flapping were greater in Pennsylvania than in Costa Rica, and during periods of straight-line soaring and gliding flight compared with circle-soaring. At both sites, flapping was more likely during rainy weather and early and late in the day compared with the middle of the day. Birds in Costa Rica flew in larger flocks than those in Pennsylvania, and birds flying in large flocks flapped less than those flying alone or in smaller flocks. In Pennsylvania, but not in Costa Rica, the number of flaps was higher when skies were overcast than when skies were clear or partly cloudy. In Costa Rica, but not in Pennsylvania, flapping decreased as temperature increased. Our results indicate that birds migrating in large flocks do so more efficiently than those flying alone and in smaller flocks, and that overall, soaring conditions are better in Costa Rica than in Pennsylvania. We discuss how differences in instantaneous migration costs at the two sites may shift the species' migration strategy from one of time minimization in Pennsylvania to one of energy minimization in Costa Rica. *Received 15 November 2005, accepted 8 July 2006.*

Each year, more than one million Broad-winged Hawks (*Buteo platypterus*) make a round-trip migration of 6,000–10,000 km along the Mesoamerican Land Corridor when traveling between their North American breeding grounds and wintering areas in Central and South America (Bildstein and Zalles 2001). Because the power requirement for continuous, flapping flight has an allometric mass exponent of 1.17 (Pennycuick 1972), large-bodied migrants are penalized compared with small-bodied migrants in that they need a disproportionately larger fat reserve to accomplish a non-stop, powered-flight migration of a given distance. As such, long-distance migration represents a potentially acute energetic challenge for large-bodied migrants such as Broad-winged Hawks (265–560 g; Goodrich et al. 1996). In fact, measures of fat reserves at the onset of migration suggest that Broad-winged Hawks do not carry the fuel supply needed to sustain powered flight between their breeding and wintering grounds without also feeding en route (Bildstein 1999).

There are two possible solutions to this energetic challenge. First, large-bodied migrants may complete their migration in stages, pausing periodically to feed and replenish fat reserves en route. Second, if their flight mechanics permit, they may significantly reduce the energetic costs associated with powered flight by relying instead on soaring and gliding flight. Although ducks, geese, and many shorebirds and landbirds exploit the first strategy (Moore 2000), Broad-winged Hawks do

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not feed substantially when migrating, particularly in the tropics (Bildstein 1999), possibly because their sit-and-wait foraging strategy does not lend itself well to the high capture rates needed for the rapid accumulation of fat reserves. Instead, they rely heavily on gliding and soaring flight to complete their long-distance movements (Smith et al. 1986). Because basal metabolic rate (BMR) increases with mass by an allometric exponent of approximately 0.75, soaring and gliding flight become increasingly cost-efficient as mass increases (Hedenström 1993). Indeed, it has been estimated that 100 g of fat would fuel powered flight for only about 5 days in Broad-winged Hawks, but it would sustain soaring flight in the species for an estimated 20 days (Smith et al. 1986).

Soaring flight is based on the conversion of the energy in atmospheric air currents into primarily potential energy (Pennycuick 1972). In North America, soaring Broad-winged Hawks gain altitude while circling in thermals and riding deflection updrafts with their wings and tails fully spread, and then gliding on flexed wings along their preferred direction of travel as they convert the altitude gained into distance traveled while seeking the next thermal or updraft along their migratory route (Kerlinger 1989). In Central America, where the species also alternately soars and glides among small thermals, it also straight-line soars and glides in the much larger tropical thermals and "thermal streets" (*sensu* Smith 1985) found in that region.

Because the distribution, abundance, and strength of thermals and updrafts are affected by topography, vegetation cover, vertical temperature gradient of the atmosphere, and intensity of solar radiation, soaring flight imposes constraints on the spatial and temporal organization of migration (Kerlinger 1989). Soaring migrants are able to migrate efficiently only when sufficient solar radiation and low cloud cover favor the production of thermals, thus concentrating individuals in specific seasonal and daily time windows. Also, in the temperate zone, thermals often occur in small, localized pockets, which sometimes force soaring birds to fly close to each other when using the same thermal. This has led some to suggest that flocking behavior occurs passively among soaring migrants, as limited spatial and temporal windows of soaring opportunity act to group the birds during their migrations (Smith 1985). Alternatively, others have speculated that soaring migrants, such as Broad-winged Hawks, actively form groups because doing so allows them to gather information (e.g., Danchin et al. 2004) about the location and strength of individual thermals passively provided by individuals traveling with them (Kerlinger 1989).

As Broad-winged Hawks travel south in autumn, it is likely that they adjust their flight behavior to accommodate changes in the abundance and strength of the thermals they encounter. At the onset of migration in late summer in the temperate zone, the sun's height in the sky and overall solar intensity begin to decline (Bildstein 1999); the strongest and greatest abundance of thermals tends to occur episodically during the several days of fair weather that typically follow the passage of cold fronts (Allen et al. 1996). Farther south in the tropics, the sun's height in the sky and solar intensity remain relatively more constant during the migration period and thermal strength appears to vary primarily as a function of local cloud cover (Smith 1980).

It has been suggested that the movements of soaring migrants are less constrained in the tropics than in the temperate zone and that their flight patterns differ in the two regions (Bildstein and Saborio 2000). For example, Fuller et al. (1998) reported that the migration speed of satellite-tracked Swainson's Hawks (*Buteo swainsoni*) soaring and gliding between breeding grounds in western North America and wintering areas in Argentina was 42% greater in the tropics than in the temperate zone. Here, we compare the flight behavior of Broad-winged Hawks at temperate and tropical sites to test three main predictions: (1) because soaring conditions are better in the tropics, birds would begin flying earlier in the day and flap less there than in the temperate zone; (2) birds within a given site would flap less at higher temperatures and less cloud cover; and (3) birds would flap less when traveling in large flocks than when traveling alone or in smaller flocks.

METHODS

We observed migrating Broad-winged Hawks in the temperate zone at Hawk Mountain Sanctuary in the Central Appalachian Mountains of eastern Pennsylvania (40° 58′ N, 74° 59′ W; 464 m ASL) on 10–28 September 2002, during peak passage at that site. Hawk Mountain straddles the 300-km-long Kittatinny Ridge, which acts as a leading line for raptor migrants in the region (Bildstein 1999). In the tropics, we observed migrating Broad-winged Hawks from a 10-m tower at the Kéköldi Indigenous Reserve, southeast of Puerto Viejo in Talamanca, Limón, Costa Rica (9° 38′ N, 82° 47′ W; 200 m ASL) on 2–19 October 2002, during peak passage at that site (Porras-Penaranda et al. 2004). The Caribbean Sea, ~2 km to the north, and the Talamanca Mountains, ~5 km to the south, funnel birds through the region's coastal lowlands, making this area one of several major concentration points along the Mesoamerican Land Corridor (Bildstein and Zalles 2001).

We used 7 × 35 binoculars and a 20–60× zoom telescope to watch birds at each site between sunrise and 18:00 EST. Individual observations were made on a focal individual during a 30-sec sample period beginning as soon as the bird was identified as a Broad-winged Hawk. The 30-sec length represented a fair trade-off between gaining a representative record of flight behavior and losing contact with the focal bird before the observation period was completed. During our observations, we recorded the number of seconds the focal individual spent (1) circle-soaring in an individual thermal and (2) straight-line soaring and gliding between thermals and along thermal streets. When circle-soaring, birds ascended thermals on fully outstretched wings with their tails fanned. When straight-line soaring and gliding, birds flew on semi-flexed wings with their wingtips and tails partly folded. We also recorded the number of flaps (i.e., individual wing beats) and used it as a measure of powered flight.

We determined flock size by counting or estimating the number of birds soaring within the same thermal or soaring and gliding in the same flight line as the focal bird. In Pennsylvania, flocks were composed of only Broad-winged Hawks. In Costa Rica, however, Broad-winged Hawks sometimes commingled with Swainson's Hawks and Turkey Vultures (*Cathartes aura*) in mixed-species flocks. We noted temperature and cloud cover (clear and partly cloudy skies versus complete overcast) at hourly intervals. We also noted time of day as time after sunrise (06:45 EST in Pennsylvania and 05:25 CST in Costa Rica) and then divided the day into three periods (early, mid, and late) to simplify analyses. At both sites, the early period included the first 4 hr after sunrise, the mid-period the next 4 hr, and the late period the next 3 hr. We did not record flight behavior later in the day.

We performed all analyses using the JMP 5.0.1 statistical package (SAS Institute, Inc. 2002). We used non-parametric Mann-Whitney *U*-tests to compare mean onset of activity and flock size between Pennsylvania and Costa Rica. To allow comparisons between soaring and gliding phases of flight, we restricted our analyses to 30-sec sequences in which the focal bird remained in one flight phase (soaring or gliding). We conducted two general analyses. The first examined which conditions enabled soaring and gliding flight without flaps. The second examined factors that influenced the extent of flapping when it did occur.

For the first analysis, we divided observations into those during which the bird did or did not flap. We ran a stepwise logistic regression that included all independent variables (site, flight phase, flock size, temperature, and cloud cover) and two-way interactions. The odds ratio (OR) measures how the fitted probability is multiplied as the regressor changes from its minimum to its maximum for continuous data, or from one category to the other for nominal data (Hosmer and Lemeshow 1989). We used the log-likelihood ratio (L-R) test to determine *P*-values. The second analysis was restricted to birds that flapped at least once while we were observing them. For each site, we conducted an ANCOVA on the number ($\log_{10}$-transformed) of flaps, according to the flock size, flight phase, temperature, and cloud cover. Data are presented as means ± SE.

RESULTS

We made 1,537 30-sec observations of Broad-winged Hawks during 13 days in Pennsylvania and 2,103 observations during 15 days in Costa Rica. In Costa Rica, flocks ranged in size from 2 to >1,000 individuals (mean = 427 ± 10; median = 140). In Pennsylvania, flock size never exceeded 350 indi-

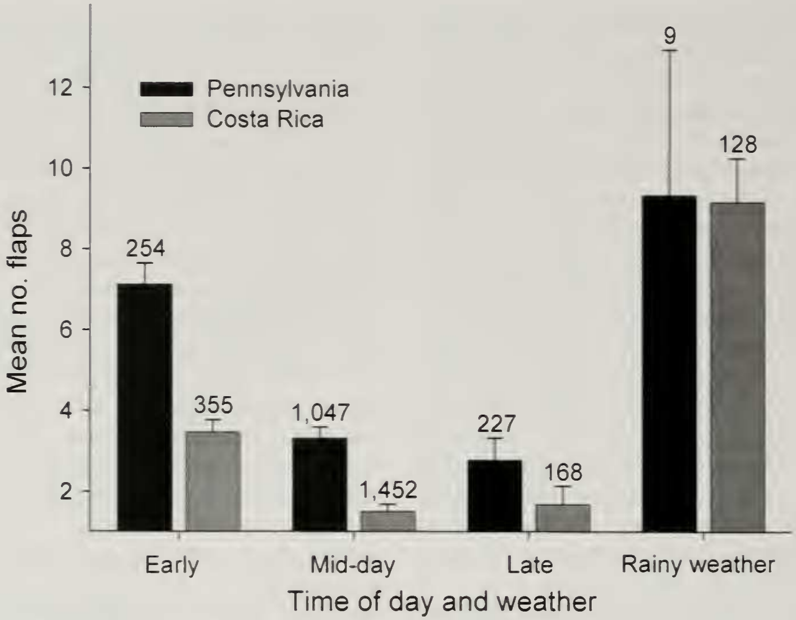

FIG. 1. Mean numbers of wing flaps per 30-sec observation period (±SE) in relation to time of day and rain condition in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. Numbers above the error bars represent sample sizes.

viduals (mean = 26 ± 1; median = 10). Overall, flock size was significantly greater in Costa Rica than in Pennsylvania (U = 1177.6, $P < 0.001$). The first migrant of the day was sighted almost one hour later in Pennsylvania than in Costa Rica (198 ± 53 min after sunrise versus 150 ± 11 min after sunrise, U = 6.32, P = 0.022), and the first individuals sighted each day were more likely to flap in Pennsylvania than in Costa Rica (35% versus 16%, L-R χ^2 = 162.7, $P < 0.001$).

TABLE 1. Results of the logistics model for the occurrence of flapping flight among Broad-winged Hawks in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002, by temperature (°C), flock size, flight type (circle or straight-line soaring), and cloud cover (overcast or not). The log-likelihood (L-R) χ^2 and P-value are shown. Sample size is 2,153.

Term	df	L-R χ^2	P
Site	1	10.24	<0.001
Temperature	1	111.56	<0.001
Site × temperature	1	55.13	<0.001
Flock size	1	16.76	<0.001
Flight type	1	77.63	<0.001
Cloud cover	1	15.24	<0.001

At both sites, birds were more likely to flap early and late in the day than at mid-day (Pennsylvania: L-R χ^2= 67.1, $P < 0.001$; Costa Rica: L-R χ^2 = 68.6, $P < 0.001$; Fig. 1). Flapping was greater during rainy periods at both sites, but significantly so only in Costa Rica (Pennsylvannia: L-R χ^2 = 3.84, P = 0.051; Costa Rica: L-R χ^2 = 78.6, $P < 0.001$). To account for these effects, we excluded from the analyses that follow any observations made early and late in the day and during rainy weather.

The logistic model indicated which conditions favored soaring flight (Table 1) and the ANCOVA identified which factors determined the extent of powered flight when it occurred (Table 2). Both extent and probability of flapping were greater during straight-line soaring and gliding than during circle-soaring (Fig. 2; OR = 0.3). The overall flapping probability was lower when birds flew in larger flocks than in smaller flocks or alone (OR = 2.8). There was no significant difference between flapping rates in Pennsylvania and Costa Rica when birds flew in flocks of up to 50 birds (L-R χ^2 = 3.75, n = 1,038, df = 1, P = 0.053); however, when birds were in flocks

TABLE 2. Comparisons of factors influencing the numbers of flaps per observation of Broad-winged Hawks in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. The ANCOVA was restricted to birds that flapped at least once during the observation.

		Pennsylvania (n = 208)		Costa Rica (n = 156)	
	df	F-ratio	P	F-ratio	P
Flock	1	0.10	0.76	9.17	0.003
Flight type	1	14.20	<0.001	18.63	<0.001
Temperature	1	1.42	0.24	8.34	0.005
Cloud cover	4	3.29	0.012	1.70	0.16

that ranged in size from 51 to 350 birds, flapping probability was significantly lower in Costa Rica than it was in Pennsylvania (L-R χ^2 = 10.25, n = 468, df = 1, P = 0.001). More than 94% of the Broad-winged Hawks seen in Costa Rica were flying in flocks of ≥50, and flapping was far more likely in Pennsylvania than it was in Costa Rica (OR = 1.87; Fig. 2). Moreover, the number of flaps decreased with flock size in Costa Rica, but not in Pennsylvania (Table 2).

Overall, the probability of flapping was greater during periods of complete overcast than it was when cloud cover was ≤75% (OR = 1.7); however, cloud cover had an effect on the number of flaps only in Pennsylvania (Table 2). Although probability of flapping decreased as temperature increased (minimum temperature = 15° C, maximum temperature = 31° C, OR = 574.1); the relationship was significantly weaker in Pennsylvania than in Costa Rica (site × temperature interaction term, OR = 0.03). Accordingly, temperature had an effect on the number of flaps in Costa Rica but not in Pennsylvania (Table 2).

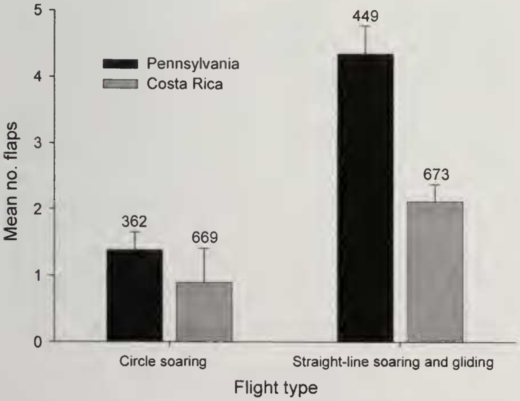

FIG. 2. Mean number of wing flaps per 30-sec observation period (± SE) made by Broad-winged Hawks in circle soaring or straight-line soaring and gliding flight in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. Numbers above the error bars represent sample sizes.

DISCUSSION

Since Huffaker (1897) first provided evidence of the existence of thermal updrafts based on observations of soaring birds, many studies have shown that avian flight can be used to gather information on meteorological processes (Shannon et al. 2002). We present our data as a biological method for measuring soaring conditions for Broad-winged Hawks traveling between the temperate zone and the tropics during southbound migration in autumn, and we offer a preliminary indication of how differences in soaring conditions affect the efficacy of migratory flight in the species.

In general, our observations confirm the flight behavior of soaring migrants documented elsewhere (Kerlinger and Gauthreaux 1985, Spaar and Bruderer 1997, Spaar et al. 1998). For example, as temperatures and solar radiation increase each morning, birds rely less on flapping flight and more on soaring and gliding flight, presumably to reduce the energetic costs of travel by taking advantage of the stronger mid-day thermals.

The negative correlation between flapping rates and flock size suggests that Broad-winged Hawks use information available in flocks to increase their flight efficiency (Kerlinger 1989). That said, although smaller flock sizes and higher flapping rates in Pennsylvania were probably due at least in part to this effect, smaller and weaker thermals in Pennsylvania also may have contributed to a greater likelihood of flapping at the site.

We suggest that migrating Broad-winged Hawks do not pursue a pure soaring and gliding strategy throughout their migration because they are constrained from doing so in two ways. First, they cannot soar when vertical airspeeds within thermals fail to reach a critical threshold value, and second, they cannot glide efficiently when inter-thermal distances exceed their maximum gliding range (Kerlinger 1989). Our data indicate that Broad-winged Hawks respond to these constraints by using powered flight preferentially during straight-line soaring and gliding flight and secondarily when circle-soaring. This tactic also has been observed in migrating Common Cranes (*Grus grus*; Pennycuick et al. 1979), as well as in other raptor species. By stretching inter-thermal glides with flapping flight, birds increase the distance realized, thereby extending their ability to reach and use the next thermal (Pennycuick 1998). Second, under certain circumstances, soaring and gliding can slow travel compared with flapping flight, particularly when the birds are soaring in small thermals. Indeed, migrants are likely to pursue a pure soaring strategy only when they have time to wait for the proper conditions and are able to move slowly along the migration corridor. For Broad-winged Hawks, time limitations may be more important in Pennsylvania than in Costa Rica, because solar intensity and photoperiod decrease rapidly during September in Pennsylvania, thereby forcing birds to move south in a brief window of time (Bildstein 1999). On the other hand, solar intensity and photoperiod remain relatively high and constant year-round in Costa Rica, resulting in a more prolonged window of time for hawk movements (Porras-Penaranda et al. 2004).

As a result, Broad-winged Hawks may be more likely to use a time-minimization strategy in temperate than in tropical zones, resulting in a higher flapping rate in Pennsylvania. Assuming an energy consumption of approximately 4 × BMR in soaring flight and a climbing rate of 1 m/sec, flight theory predicts that during time-minimizing migration, heavy birds (>132 g) should switch from soaring to flapping flight (Hedenström 1993). For energy-minimizing migration, the switch from soaring to flapping flight occurs at a lower climbing rate. Thus, as the rate of climbing decreases, time-minimizing migrants should switch from soaring to flapping flight sooner than energy-minimizing migrants (Hedenström 1993). These temporal and energetic aspects may explain why Broad-winged Hawks are more likely to resort to flapping in Pennsylvania than in Costa Rica.

Our observations indicate that Broad-winged Hawks shift from a mixed strategy of soaring and gliding supplemented by powered flight to a nearly pure strategy of soaring and gliding as they proceed during their southbound migrations, suggesting that the instantaneous metabolic cost of migration declines from north to south. By relying more on powered flight in the north, where conditions are less favorable for soaring, Broad-winged Hawks may trade off energy against time, a phenomenon also observed in Levant Sparrowhawks (*Accipiter brevipes*; Spaar et al. 1998). This would allow them to move along the corridor at a faster rate at the expense of depleting fat reserves.

Finally, we highlight the fact that we did not discriminate adult from juvenile Broad-winged Hawks, and that we observed migrants at only two sites. Additional observations in which the flight behavior of adults and juveniles are compared and in which other species are observed at other temperate and tropical sites are likely to provide important insights into the extent to which age and latitudinal geography affects the flight behavior of migrating birds of prey.

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